15. T. E. Martin, *Ecol. Monogr.* **65**, 101–127 (1995).
16. V. Remeŝ, T. E. Martin, *Evolution* **56**, 2505–2518 (2002).
17. T. E. Martin, J. C. Oteyza, A. E. Mitchell, A. L. Potticary, P. Lloyd, *Am. Nat.* **185**, 380–389 (2015).
18. Z. Wang *et al.*, *Evolution* **68**, 81–91 (2014).
19. T. E. Martin, *Am. Nat.* **183**, 313–324 (2014).
20. T. B. Watkins, *Physiol. Zool.* **69**, 154–167 (1996).
21. D. B. Miles, *Evol. Ecol. Res.* **6**, 63–75 (2004).
22. K. O. Perez, S. B. Munch, *Funct. Ecol.* 10.1111/1365-2435.12343 (2014).
23. K. P. Dial, R. J. Randall, T. R. Dial, *Bioscience* **56**, 437–445 (2006).
24. K. W. Morrison, J. M. Hipfner, C. Gjerdrum, D. J. Green, *Condor* **111**, 433–441 (2009).
25. R. D. Dawson, C. C. Lawrie, E. L. O'Brien, *Oecologia* **144**, 499–507 (2005).
26. B. E. Sæther, *Ornis Scand.* **20**, 13–21 (1989).
27. C. E. Tarwater, R. E. Ricklefs, J. D. Maddox, J. D. Brawn, *Ecology* **92**, 1271–1281 (2011).

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SUPPLEMENTARY MATERIALS

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Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism

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The global biogeography of microorganisms remains largely unknown, in contrast to the well-studied diversity patterns of macroorganisms. We used arbuscular mycorrhizal (AM) fungus DNA from 1014 plant-root samples collected worldwide to determine the global distribution of these plant symbionts. We found that AM fungal communities reflected local environmental conditions and the spatial distance between sites. However, despite AM fungi apparently possessing limited dispersal ability, we found 93% of taxa on multiple continents and 34% on all six continents surveyed. This contrasts with the high spatial turnover of other fungal taxa and with the endemism displayed by plants at the global scale. We suggest that the biogeography of AM fungi is driven by unexpectedly efficient dispersal, probably via both abiotic and biotic vectors, including humans.

The arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are an ancient but species-poor group of root symbionts whose origin coincided with the first appearance of land plants (*1*). The AM symbiosis involves ~80% of land plants and ~250 morphologically defined or 350 to 1000 molecularly defined AM fungi (*2*, *3*). The relationship typically allows the fungus to receive plant-synthesized carbon, while conferring the plant with an increased capacity for nutrient capture and improved tolerance of drought and pathogens (*4*). At a wider scale, the symbiosis influences plant-plant interactions and the structure of plant communities, and thus it can affect agricultural production and the conservation and restoration of ecosystems (*5*). Because many AM fungi are unculturable, identification of AM fungal taxa in the environment is principally dependent on DNA-based methods; these asexual organisms are classified into approximately species-level taxonomic units using clustering or sequence-matching algorithms (*6*). The recent rapid development of DNA sequencing technology is allowing detection of increasing numbers of AM fungi and other microorganisms in environmental samples and enabling their responses to local and regional environmental gradients to be recorded (*7*–*9*). However, knowledge about global AM fungal diversity is piecemeal. This is partly because most classification approaches generate operational taxonomic units (OTUs) that cannot be readily compared between different studies or study areas (*2*, *10*). Additionally, the communities of AM fungi present in many geographic regions, biomes, and ecosystems remain entirely unstudied (*11*, *12*).

Although empirical data concerning AM fungal dispersal are limited, the process is believed to be mostly local and mediated by invertebrates (*4*, *13*), with some evidence of small mammals, water, and human activities (e.g., agricultural practices) dispersing propagules farther (*14*–*16*). As yet, there is no direct evidence of efficient long-distance dispersal (*13*, *17*). Hence, extensive global sampling of AM fungal diversity should reveal high endemism and similar responses to environmental conditions as those shown to drive local-scale diversity (*7*, *8*). We used high-throughput sequencing of environmental samples to survey AM fungal diversity and distribution in natural ecosystems worldwide. We examined the contributions of environmental conditions, spatial distance between plots, paleogeographic history, and plant-host identity on AM fungal diversity at local to global scales.

We collected 1014 individual root samples from vegetation plots worldwide and identified DNA-based AM fungal taxa ["virtual taxa" (VT), after (*10*)] in plant roots by using 454 sequencing. VT are phylogenetically defined sequence groups that exhibit a taxonomic resolution similar to that of morphological species, or above that resolution in some AM fungal families (*11*). As in traditional binomial nomenclature, the VT classification applies consistent principles to taxonomic assignments across data sets and provides comparability between studies. We used 912,515 quality-filtered AM fungal reads, representing 836 samples, 161 plant species, and 67 plots, for further analysis (Fig. 1A, fig. S1, tables S1 to S3, and database S1). We recorded 236 (68%) of the 348 currently known AM fungal VT and identified a further 10 taxa that were previously undescribed (fig. S2). Ninety-three percent of recorded VT were present on more than one continent, and one-third (34%) were present on all six sampled continents. Furthermore, 90% of VT were found in more than one climatic zone, and 79% were found in both forests and grasslands (the two most widely sampled ecosystems) (Fig. 1B). We added published data on AM fungal VT distribution from the Maarj*AM* database (*10*) to create a comprehensive data set containing all available VT records. We compared this data set with the distribution of plants (the AM fungus host organisms) for which global data are available at the family (*18*) but not the species level. The mean fractions of the AM fungal taxon pool found on individual continents (57%) and of shared

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VT recorded from pairs of continents (56%) were similar to the respective values for plant families (59% in both cases) (Fig. 1, C and D). Using available data on plant species diversity, we estimated that the mean proportion of plant species shared between pairs of continents is at least an order of magnitude lower (~4%) (Fig. 1, C and D).

Cosmopolitan organismal distribution may occur if speciation events representing the origins of extant taxa happened before major continental reconfigurations (i.e., ancient vicariance); it may also occur as a result of efficient global dispersal (*16*). Where ancient vicariance is the primary driver, taxa with an origination time after putative vicariance events should display restricted distributions. We used distribution data for AM fungal VT, along with a dated phylogenetic tree reconstructed using small subunit ribosomal RNA (SSU rRNA) gene sequence data, to show that most VT had origination times after the major continental shifts occurred; in addition, we found that the collective descendant taxa of all but the most recent ancestral nodes are globally distributed (Fig. 2 and figs. S3 and S4). Though it was derived from a fossil-calibrated single-gene analysis, this pattern strongly suggests that the wide distribution of AM fungal VT is driven by efficient recent dispersal rather than by ancient vicariance. Integrating this finding with the current understanding of AM fungal ecology requires a reassessment of potential dispersal mechanisms. First, the frequency of long-distance dispersal events mediated by known agents, including wind (*13*, *19*) and human activities (*16*), may have been underestimated owing to a lack of empirical data. Second, overlooked dispersal agents might be responsible for substantial propagule transport. For example, although there is no quantitative evidence concerning dispersal in seawater or via birds (*20*), these agents might explain the abundance of AM fungi on oceanic islands (*21*). Third, rare dispersal events, such as powerful dust storms, may strongly influence distribution patterns, because AM fungal propagules exhibit high viability. Given that AM fungal spores are generally large and demonstrate high survival rates in harsh environmental conditions (*4*, *22*), they might form a propagule bank that can efficiently exploit favorable conditions even if these are encountered infrequently, analogous to large-seeded plants (*23*) and sporocarp-forming ectomycorrhizal fungi (*24*).

To disentangle the effects on AM fungal communities of biotic and abiotic ecosystem components and of spatial processes, we partitioned variation in AM fungal richness and community composition between sets of variables related to paleogeography, spatial distance between plots, environment, and plant host (figs. S5 to S7 and tables S4 to S6). We found that the richness of AM fungal communities in individual plant roots or vegetation plots varied in relation to spatial distance and environmental gradients (Fig. 3A and fig. S8), consistent with existing evidence (*3*, *7*, *8*). However, our data showed that the taxon richness (alpha diversity) of AM fungal communities decreases with latitude (Fig. 3E), a pattern that is widespread in macroorganisms (*25*) but is not observed among ectomycorrhizal fungi (*12*, *26*) or other soil microbes (*27*). Environmental variables explained slightly more of the variation in plot and sample richness than spatial distance did, but most variation was explained by the intersection of these variable sets (i.e., environmental gradients that exhibit a spatial lag, such as temperature) (table S4). AM fungal community richness was consistently higher in grasslands than in forests (Fig. 3E), whereas the converse was true of the local taxon

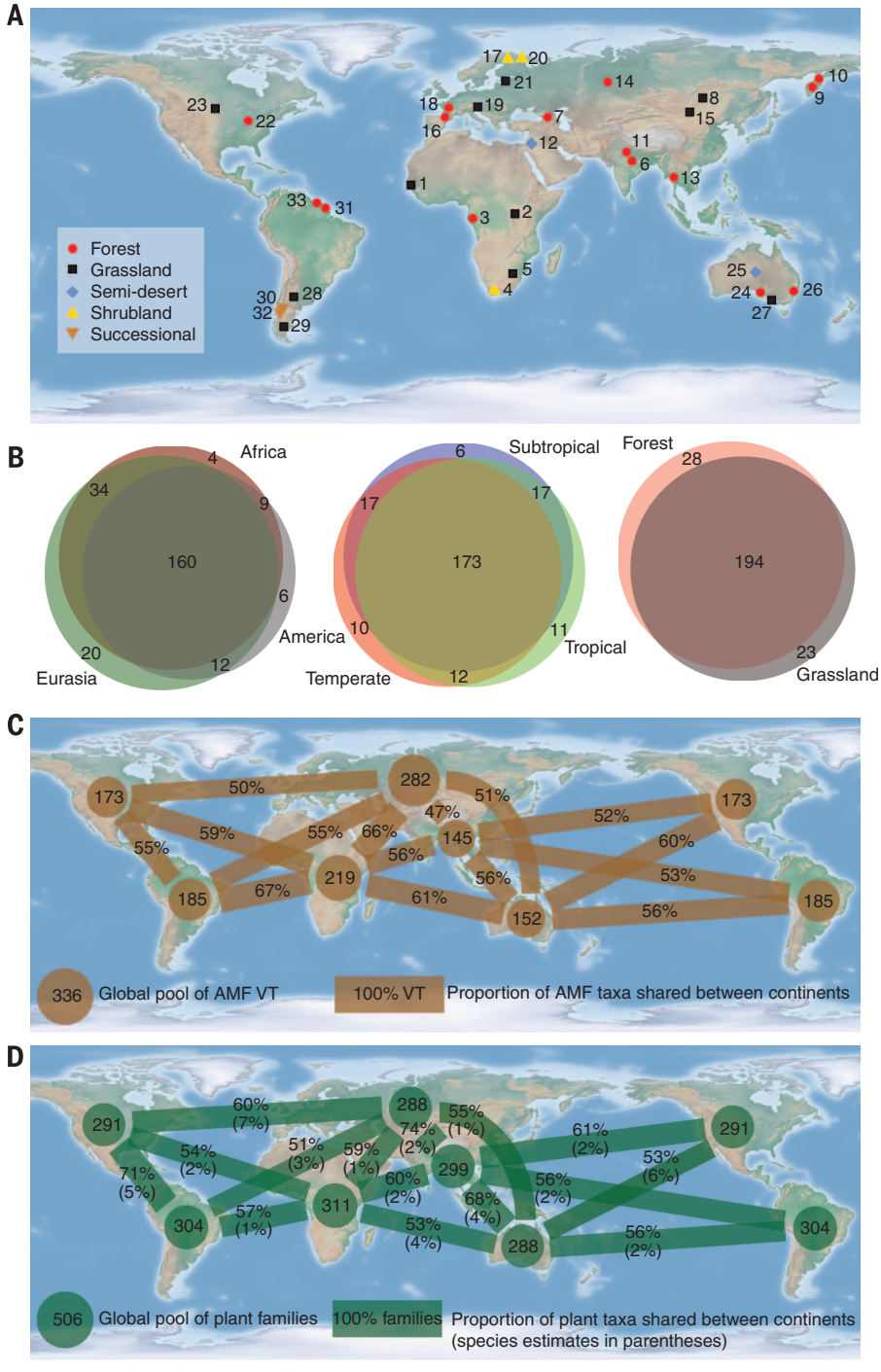

Fig. 1. Global biogeography in AM fungi and plants. (**A**) Sampled sites (table S1). (**B**) Venn diagrams (using relevant subsets of the full data set) showing the sharing of AM fungal VT between continents, biomes, and ecosystems. (**C**) Counts of VT and (**D**) plant families found on each continent (circles) and the percentages shared between different continents (lines). The areas of circles and thicknesses of lines are respectively proportional to the fraction of the global taxon pool represented and the fraction of taxa shared between pairs of continents. Shared-species estimates for continent pairs are shown in parentheses in (D). (C) also includes distribution data from the Maarj*AM* database of published SSU rRNA gene sequences (*10*) for AM fungal VT with at least one known geographic point of origin.

turnover rate (beta diversity) (Fig. 3F), and the total richness (gamma diversity) recorded in the two habitats was similar (Fig. 1B). Thus, despite grassland biomes having originated during the Eocene (making them an order of magnitude younger than the first AM fungi) (*28*), they have become a favorable habitat for AM fungi. Vascular plants exhibit a similar pattern: Higher small-scale richness is observed in grasslands (*29*), but total richness is higher in forests (*30*).

Spatial distance explained at least as much plot-level variation in community composition as did environmental variables (Fig. 3, B and C; table S6). The role of local-scale dispersal limitation in structuring AM fungal communities has previously been recognized (*7*); here, we provide empirical evidence of distance decay on a global scale. Sample-level community composition was additionally explained by paleogeographic history and host-plant phylogeny, though the explanatory power of these variable sets was very low (Fig. 3C). Although the idea that AM fungal community composition contains a paleogeographic signature has previously been proposed (*31*), our analysis represents the first empirical evidence to support this theory. The best-fitting predictor variables related to the plant host suggested that AM fungal community composition responds to the coarsest-scale differences in plant phylogeny (fig. S6). Previous research (*32*) found that AM fungal community structure converges as the phylogenetic distance between host plants increases; our study demonstrates the converse pattern.

Because biogeographic analyses are highly dependent on taxonomic resolution (*33*), we repeated our analyses using a second widely used approach for sequence identification: de novo clustering of OTUs at 97% sequence similarity (figs. S1 and S9). The recorded degree of endemism among OTUs (fig. S10) was higher than that of VT and plant families, but it was approximately an order of magnitude lower than that estimated for plant species (Fig. 1D). Variations in AM fungal richness and community composition were similar across the two approaches used for sequence identification (fig. S11) [similar findings are presented in (*34*)]. Furthermore, rarefaction, as a means of standardizing the sequencing effort between samples, made a negligible difference to the results of community richness and composition analyses (fig. S11).

We have demonstrated for an important terrestrial microbial group that local environmental conditions and spatial configurations determine the composition of communities. AM fungal taxa are known to differ in their habitat preferences (*35*) and responses to local environmental gradients (*7*–*9*), and unfavorable environmental conditions are a likely factor limiting within-region dispersal of AM fungal taxa with particular ecological requirements (*8*, *35*). This bears a warning message, because progressive habitat loss and fragmentation of landscapes might result in a situation where human-induced dispersal barriers, such as agricultural systems with few potential

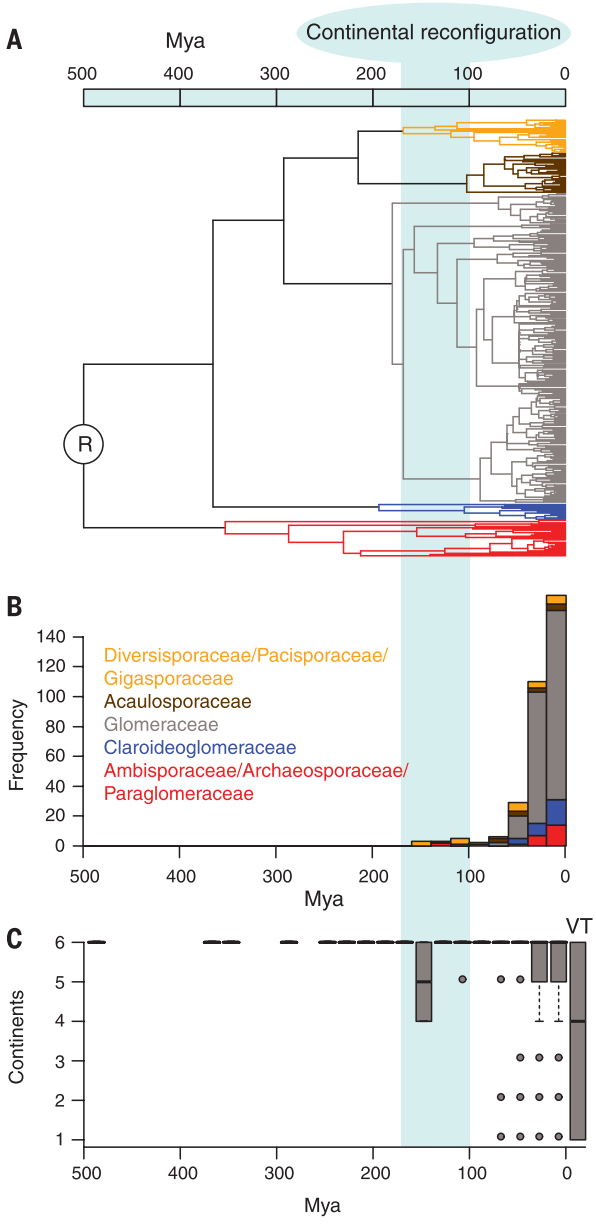

Fig. 2. Phylogeny-based analysis of AM fungal distribution. (**A**) Bayesian phylogenetic tree of AM fungi, with family groupings shown in different colors. Tree tips represent VT type (i.e., representative) sequences. (**B**) Mean ages of nodes immediately ancestral to VT, as estimates of VT origination times. (**C**) Number of continents occupied by the descendant taxa of internal tree nodes (i.e., ancestral taxa). The median (central bar), quartiles (gray box), ranges excluding outliers (whiskers), and outliers (points) of the continental distributions are shown for nodes over 20-million-year increments. The right-most boxplot shows the continental distribution of tree tips (VT). VT distribution was determined using data from this study and from the Maarj*AM* database (*10*) for VT with at least one known geographic point of origin. Timing was derived by using a relaxed clock analysis with fossil calibration of the root [R in (A)] at 505 million years ago (Mya). The vertical blue band across panels shows the timing of continental reconfiguration events, according to (*40*).

mutualist partners, inhibit the arrival of symbiotic fungi that are necessary for ecosystem functioning and service provision. We showed that the cosmopolitan distribution pattern of AM fungal taxa contrasts with that of their host plants at the species level, whereas the host plants exhibit a similar pattern at a taxonomic rank several levels higher (*18*). At a continental scale, this pattern also contrasts with the high spatial turnover of some microbial organisms, including fungi (*36*, *37*), but it resembles observed patterns for certain bacteria (*38*). We propose that earlier reports of patchily distributed AM fungal taxa at the continental or global scales may have been related to low sampling effort (*11*) and/or the collation of methodologically diverse data (*3*, *10*). We suggest

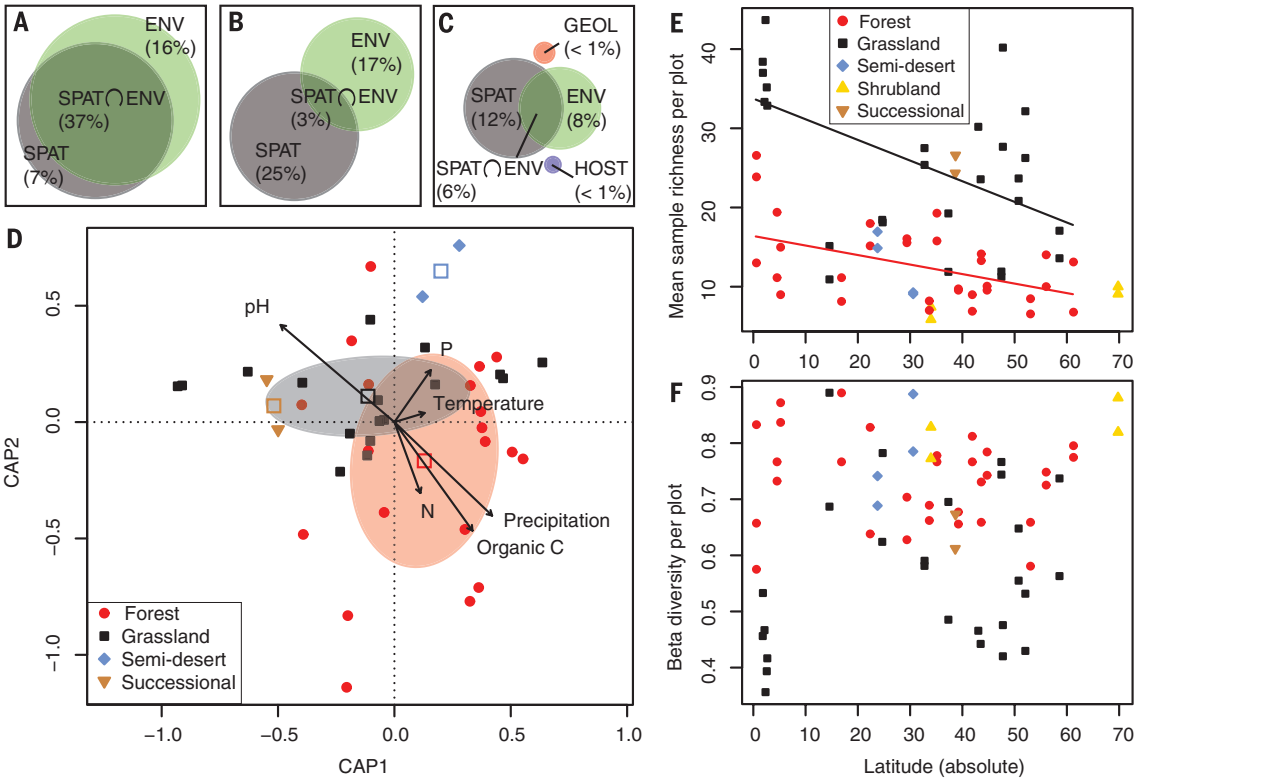

Fig. 3. Variation in AM fungal community richness and composition related to paleogeography (GEOL), spatial distance (SPAT), environment (ENV), and plant host (HOST). (**A**) Richness per plot. (**B**) Qualitative community composition per plot. (**C**) Qualitative community composition per sample. (**D**) Spatially constrained, distance-based redundancy analysis of plot-based qualitative community composition. Ecosystem centroids (open squares) and dispersions (ellipses, 1 SD around forest and grassland centroids) are shown. Arrows indicate the direction of the maximum change in environmental variables. (**E**) Alpha diversity (mean sample richness) per plot (absolute latitude: F = 11.5, P = 0.002; ecosystem: F = 30.9, P < 0.001; interaction: F = 1.4, P = 0.25). Only forest and grassland plots were analyzed. Lines are model-predicted values of richness at a range of latitudes. (**F**) Beta diversity (mean Sørensen index between sample pairs) per plot (absolute latitude: F = 0.7, P = 0.40; ecosystem: F = 23.7, P < 0.001; interaction: F = 2.4, P = 0.14). In (A) through (C), ∩ indicates the intersection of variable sets and is shown when >1%; the size of each component is proportional to the fraction of the variation explained.

that addressing both global and local dispersal of AM fungi and the role of dispersal agents such as birds, large mammals (including humans), wind, surface water, and seawater can illuminate the processes governing AM fungal diversity patterns. Along with a better understanding of the functional attributes of cosmopolitan taxa throughout their ranges (*39*), such information will not only enhance our understanding of microbial biogeography but will also facilitate ecosystem restoration and sustainable agriculture.

REFERENCES AND NOTES

1. P. Bonfante, A. Genre, *Trends Plant Sci.* **13**, 492–498 (2008).
2. M. Öpik, J. Davison, M. Moora, M. Zobel, *Botany* **92**, 135–147 (2014).
3. S. N. Kivlin, C. V. Hawkes, K. K. Treseder, *Soil Biol. Biochem.* **43**, 2294–2303 (2011).
4. S. E. Smith, D. J. Read, *Mycorrhizal Symbiosis* (Academic Press, Amsterdam, ed. 3, 2008).
5. M. G. A. van der Heijden, R. D. Bardgett, N. M. van Straalen, *Ecol. Lett.* **11**, 296–310 (2008).
6. H. M. Bik *et al.*, *Trends Ecol. Evol.* **27**, 233–243 (2012).
7. A. J. Dumbrell, M. Nelson, T. Helgason, C. Dytham, A. H. Fitter, *ISME J.* **4**, 337–345 (2010).
8. C. Hazard *et al.*, *ISME J.* **7**, 498–508 (2013).
9. Y. Lekberg, J. Meadow, J. R. Rohr, D. Redecker, C. A. Zabinski, *Ecology* **92**, 1292–1302 (2011).
10. M. Öpik *et al.*, *New Phytol.* **188**, 223–241 (2010).
11. M. Öpik *et al.*, *Mycorrhiza* **23**, 411–430 (2013).
12. L. Tedersoo *et al.*, *Science* **346**, 1256688 (2014).
13. C. Egan, D. W. Li, J. N. Klironomos, *Fungal Ecol.* **12**, 26–31 (2014).
14. S. A. Mangan, G. H. Adler, *Oecologia* **131**, 587–597 (2002).
15. M. J. Harner, N. Opitz, K. Geluso, K. Tockner, M. C. Rillig, *Aquat. Sci.* **73**, 35–42 (2011).
16. S. Rosendahl, P. McGee, J. B. Morton, *Mol. Ecol.* **18**, 4316–4329 (2009).
17. S. N. Kivlin, G. C. Winston, M. L. Goulden, K. K. Treseder, *Fungal Ecol.* **12**, 14–25 (2014).
18. V. H. Heywood, R. K. Brummitt, A. Culham, O. Seberg, *Flowering Plant Families of the World* (Kew Publishing, Richmond, UK, 2007).
19. N. J. Warner, M. F. Allen, J. A. MacMahon, *Mycologia* **79**, 721–730 (1987).
20. W. D. McIlveen, H. Cole Jr., *Can. J. Bot.* **54**, 1486–1489 (1976).
21. R. E. Koske, J. N. Gemma, *Am. J. Bot.* **77**, 466–474 (1990).
22. S. Varga, C. Finozzi, M. Vestberg, M.-M. Kytöviita, *Mycorrhiza* **25**, 335–343 (2015).
23. J. Metz *et al.*, *J. Ecol.* **98**, 697–704 (2010).
24. S. I. Glassman *et al.*, *New Phytol.* **205**, 1619–1631 (2015).
25. H. Hillebrand, *Am. Nat.* **163**, 192–211 (2004).
26. L. Tedersoo *et al.*, *Mol. Ecol.* **21**, 4160–4170 (2012).
27. R. D. Bardgett, W. H. van der Putten, *Nature* **515**, 505–511 (2014).
28. G. J. Bredenkamp, F. Spada, E. Kazmierczak, *Plant Ecol.* **163**, 209–229 (2002).
29. J. B. Wilson, R. K. Peet, J. Dengler, M. Pärtel, *J. Veg. Sci.* **23**, 796–802 (2012).
30. G. Kier *et al.*, *J. Biogeogr.* **32**, 1107–1116 (2005).
31. J. B. Morton, S. P. Bentivenga, J. D. Bever, *Can. J. Bot.* **73**, 25–32 (1995).
32. S. D. Veresoglou, M. Rillig, *Plant Soil* **377**, 395–406 (2014).
33. C. A. Hanson, J. A. Fuhrman, M. C. Horner-Devine, J. B. H. Martiny, *Nat. Rev. Microbiol.* **10**, 497–506 (2012).
34. Y. Lekberg, S. M. Gibbons, S. Rosendahl, *New Phytol.* **202**, 1101–1104 (2014).
35. T. Helgason, A. H. Fitter, *J. Exp. Bot.* **60**, 2465–2480 (2009).
36. A. Meiser, M. Bálint, I. Schmitt, *New Phytol.* **201**, 623–635 (2014).
37. J. M. Talbot *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6341–6346 (2014).
38. J. B. H. Martiny, J. A. Eisen, K. Penn, S. D. Allison, M. C. Horner-Devine, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 7850–7854 (2011).
39. P. L. Chagnon, R. L. Bradley, H. Maherali, J. N. Klironomos, *Trends Plant Sci.* **18**, 484–491 (2013).
40. A. Schettino, C. R. Scotese, *Geophys. J. Int.* **163**, 727–759 (2005).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S11
Tables S1 to S6
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References (*41–84*)

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Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism

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